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# CONTROL OF NITROGEN MINERALIZATION IN A SAGEBRUSH STEPPE LANDSCAPE

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RUNNING HEAD: N Mineralization in a Sagebrush Steppe

### Abstract

Factors controlling N turnover in sagebrush ecosystems are separable into two groups. The first group comprises properties having strong spatial patterning at a landscape scale, but being temporally static at time scales of years or tens of years. These static properties include plant species assemblages, total soil nutrient pools, and soil texture. A second group includes properties that vary across the landscape over shorter time scales, i.e. annually, seasonally, and diurnally. These dynamic properties include soil moisture, temperature, and amount of available nutrients. This paper evaluates the landscape variability of properties in both of these groups, and examines the extent to which these factors control N turnover.

Static ecosystem properties were entered into a principal components analysis resulting in four axes of landscape variability. A statistical analysis of the relationship of net N mineralization with the principal components and with soil temperature and moisture suggested that soil microclimate and organic matter quality both control in situ N turnover. Soil microclimate limited N mineralization to a short season in early spring and summer; only during this time did soil organic matter exert control. In landscape positions where soil organic matter pools were low, improved soil microclimate conditions did not increase N mineralization rates. A similar approach may be useful in evaluating control over ecosystem processes in other systems that are characterized by strong seasonal and spatial variability.

## Introduction

Organic matter quantity and quality interact with soil microclimate to control biogeochemical cycling in semiarid ecosystems. At a small scale, shrub-intershrub variability in organic matter content has been shown to control nutrient turnover in many semiarid shrubland systems (Charley and West 1975, 1977, Klopatek 1987, Lajtha and Schlesinger 1986). At a larger scale, aeolian and fluvial erosion-deposition processes result in landscape gradients in organic matter quality and content and nutrient supply (Schimel 1986b, Lajtha and Schlesinger 1988). Nutrient dynamics in semiarid ecosystems are also closely linked to seasonal variation in temperature and moisture. Several authors have suggested the importance of seasonal and pulsed moisture to nutrient availability and N mineralization (Fisher et al. 1987, Schimel and Parton 1986). During short periods when soil moisture is adequate, nutrient supply to plant growth has been shown to be limiting in arid and semiarid ecosystems (Sturges 1986, James and Jurinak 1978, Ettershank et al. 1978). Any evaluation of controls over biogeochemical cycling processes in semiarid systems must therefore address spatial variation in relatively static soil properties such as soil organic matter, as well as relatively dynamic factors such as soil microclimate.

The purpose of this paper is to examine the interactions between soil microclimate and organic matter as they control N mineralization in a semiarid sagebrush steppe. High-elevation

sagebrush ecosystems of Wyoming are an especially good place to evaluate control of semiarid ecosystem processes. These systems typically have marked topographic variability. Strong winter winds redistribute snow, causing large spatial as well as seasonal variation in soil moisture and soil temperature. Over the long term, repeated landscape patterns of soil moisture and temperature lead to relatively stable patterns in plant species assemblages, primary production, and organic matter quality and quantity across the landscape.

I suggest that two sets of ecosystem controls with different characteristic rates of change interact to control N mineralization in this ecosystem. These are the slowly changing control by substrate availability (static control), and the rapidly changing control by soil microclimate (dynamic control). A conceptual model incorporating this approach to the spatial and temporal control of ecosystem properties in a sagebrush landscape is illustrated in Figure 1. The elements of that conceptual model are:

- a. During the winter months, wind and topography interact to create a strong gradient in snow accumulation across the landscape. During the growing season, soil moisture and soil temperature vary significantly with landscape position, and the magnitude of variability is greatest in spring.
- b. Long-term patterns in plant productivity are the primary

factors governing the quantity of soil organic matter pools. As a result, soil nitrogen and carbon pools vary significantly across the landscape, with all pools increasing with vegetation cover and with downslope and leeward position. The same process occurs at a smaller scale, so that C and N are higher under shrubs than between shrubs.

c. Over the long term, slope processes result in net movement of fine soil materials from upper to lower slope positions. Because of this, soil clay content increases with downslope and leeward position and with increasing vegetation cover. Phosphorus distributions across the landscape also are controlled by the long-term movement of fine material across the landscape, so that P content correlates with clay content.

d. Short-term variation in soil microclimate (a. above) controls net N mineralization as it varies both seasonally and spatially.

e. As a result of a, b, and c above, organic substrate availability for N mineralization increases with downslope and leeward position. Net N mineralization varies significantly across the landscape because of higher substrate availability, with higher rates occurring in net deposition areas. Spatial variability in N mineralization

is highest when soil moisture and temperature show the greatest spatial variability.

Each of these hypotheses is formulated and tested as a statistical hypothesis. These results are then used to evaluate the interaction between soil microclimate and organic matter as controls over N mineralization.

## Methods

### Study Area Description

My research was conducted at the Stratton Sagebrush Hydrology Study Area (Stratton), located 29 km west of the town of Saratoga, Wyoming (107° 10' W longitude, 41° 25' N latitude). Stratton is located on a dissected plateau of Tertiary origin at an average elevation of 2400 m (Sturges 1975). The underlying substrate is the Brown's Park Formation, a weak tuffaceous sandstone (Love and Christianson 1985). Soils of the region are generally Argic Cryoborolls (Sturges 1986) that vary across the landscape with A horizons deepest in drainages and deposition areas and most shallow in windswept and erosional areas (Burke et al. 1987).

The climate and topography at Stratton are characteristic of the high elevation mountain big sagebrush (Artemisia tridentata ssp. vaseyana) systems in the Intermountain Sagebrush Steppe (West 1983) throughout Wyoming. The mean annual temperature is 2.7° C (Sturges 1982). Wind speeds average 5.3 m/sec and are highest in the winter (Sturges 1986). Precipitation at Stratton

averages 525 mm annually; two thirds of this amount falls as snow (Sturges 1977). Deep drifts accumulate in topographic depressions such as drainages and nivation hollows on leeward slopes. Vegetation can contribute to snow accumulation on exposed sites (Sturges 1975), but topography is the master control of snow distribution. Late winter snow accumulations range from 5 cm on windward slopes to > 6 m in topographic depressions (Sturges 1975).

Plant species distribution is controlled by snow distribution patterns at Stratton. In areas of deepest snow accumulation (nivation hollows), sagebrush is eliminated by a snow mold specific to sagebrush (Sturges and Nelson 1984, Nelson and Sturges 1986), and by curtailed growing season. These areas are dominated by grasses such as Agropyron smithii, Stipa viridula, and Leucopoa kingii. Along drainages and on leeward slopes where snow accumulations are moderate to deep, Artemisia tridentata ssp. vaseyana (mountain big sagebrush; subspecies nomenclature after Beetle 1960 and Beetle and Young 1965) is the dominant shrub species and Festuca idahoensis the major grass. On slightly more windward slopes, the shorter big sagebrush subspecies Artemisia tridentata ssp. wyomingensis (Wyoming big sagebrush) is dominant, typically mixed with Koeleria cristata and Poa species. On windward exposures, where snow accumulation and soil moisture are least, Artemisia nova (black sagebrush), a short, nearly prostrate shrub, is mixed with cushion-forming

plants such as Arenaria hookerii, Happlopappus acaulis, and Phlox hoodii. Dry windswept ridges are characterized by a sparse cover of cushion plants

Because vegetation is clearly related to landscape position (Burke et al. submitted), I use vegetation as an index of landscape position throughout this paper. For much of the paper, data are summarized for three vegetation types: an Artemisia tridentata ssp. vaseyana (ARTRV) vegetation type representing toeslope or net deposition areas (90% shrub cover), an Artemisia tridentata ssp. wyomingensis (ARTRW) vegetation type representing moderately exposed slopes (50% shrub cover), and an Artemisia nova (ARNO) vegetation type representing exposed ridgetops (20% shrub cover). In other analyses, continuous data used are shrub species cover and total grass and cushion plant cover.

#### Summary of field sampling plan

Soil properties were sampled to obtain continuous data across the landscape. Eighty-nine 5 x 5m plots were located using a stratified random process on an area of 360 x 960 m that bisects the Loco Creek watershed to characterize vegetation patterns (Burke et al. submitted). Thirty plots were chosen from these 89 for soil studies using a stratified random method to represent the vegetation variability. These 30 plots were used in all sampling for soil texture, total carbon, nitrogen, and phosphorus, and for in situ measurements of N mineralization during the months of June, July, and August 1985, winter 1985-86,



April, and May 1986. For the months of June, July, August, September, and October 1986, a subset of 9 plots was used for in situ incubations, with three plots in each of the three vegetation types ARTRV, ARTRW, and ARNO.

All measurements in the plots were stratified into between and under-shrub locations, defined by canopy boundaries. Interspaces vary in size and plant cover among the vegetation types; ARNO vegetation has large interspaces (about 1 shrub unit) that a ground, and ARTRV vegetation has relatively small interspaces (> 5 shrub units) with a high grass cover. Calculations of nutrients pools ( $\text{g/m}^2$ ) are weighted by shrub cover to account for this difference.

#### Soil pool and texture determinations

Soil cores were collected from each of the 30 plots in the summer of 1985. Samples were collected at two depths (0-5 cm and 5-15 cm), and in two positions (under shrubs and between shrubs) with two replicates per combination. Under-shrub samples were taken randomly under the sagebrush canopy; between-shrub samples were taken randomly outside sagebrush canopy areas.

In the lab, samples were air-dried to constant moisture, weighed, sieved through a 2 mm sieve, and the fine fraction reweighed. Total soil mass and mass of fines were used to calculate bulk density (Blake 1965) and fine soil density (fine soil in  $\text{g/cm}^3$ ). Six subsamples were weighed from the fine fraction and processed as follows. One subsample was oven-dried

at 70° C for moisture correction. Two subsamples were analyzed for carbon. Two subsamples were oven-dried and analyzed for total nitrogen and phosphorus. Finally, one subsample was analyzed for texture.

Total carbon (C) and inorganic carbon were determined using a wet oxidation/diffusion procedure described by Snyder and Trofymow (1984). Inorganic carbon was never greater than 3% of total carbon, averaging 0.2% of C, and could generally not be resolved from the blank. Samples were digested for N and P analysis using a persulfate peroxide block digestion procedure and analyzed on a Scientific Instruments continuous flow autoanalyzer. Soil texture was determined using a hydrometer procedure described by Day (1965).

#### In situ incubations

Net in situ nitrogen mineralization rates were estimated using a buried bag procedure (Ellenberg 1977). Each month, 6 soil cores from a 5-15 cm depth were collected from each plot (30 plots for June 1985 - May 1986, 9 plots for June 1986 - October 1986, as described above). Three cores were randomly located under shrubs and three between shrubs. Each core was placed in a large bag, mixed thoroughly, and hand-sorted to remove all organic debris larger than 2 mm. A subsample was placed into a small plastic bag, placed into the core hole, and covered with 5 cm of soil. The remainder of the sample was returned to the lab for nitrate and ammonium determinations. At the same time,

"final" buried bag samples from the previous month were collected and returned to the lab. Buried bags were left in place for 30 days, except winter samples, which incubated from September 1985 through March 1986. Nitrate and ammonium concentrations were determined using KCl extraction and colorimetric analysis. Extracts were preserved with phenyl mercuric acetate and acidified, and analyzed using the standard continuous flow analyzer colorimetric procedure for nitrate and ammonium.

Net nitrification was calculated as the difference in nitrate content between the initial and final buried bag samples. Net N mineralization was calculated as the sum of net ammonium production and net nitrification. These rates and initial ammonium and nitrate contents were converted to a mass basis ( $\text{g N/m}^2$  soil) using bulk density for the fine fraction soil and weighting the under- and between-shrub data by shrub cover to arrive at a total plot value.

Soil moisture measurements corresponding to the monthly in situ incubations were made on the individual buried bag samples themselves. Averages of daily maximum air temperatures for each month (data from Sturges, personal communication) were also available for analysis.

#### Field temperature and moisture measurements

I measured soil temperature and moisture in 9 plots, 3 representing each vegetation type, from May 1986 through October 1986 at one-week intervals. Measurements were made once daily,

but occasionally I made multiple measurements during the day to see diurnal variation under different weather conditions. Soil moisture samples were taken outside but close to the plots, from 0-15 cm depth both under and between shrubs for each plot. Soil temperatures were measured at a 10-cm depth.

### Statistical procedures

Each of the hypotheses enumerated above (a-e) was tested as a statistical hypothesis. Soil moisture and temperature (hypothesis a) were examined by analysis of variance (SYSTAT 1984). Plots were grouped by vegetation type, and the significance of vegetation type and shrub position was tested for each date. Hypothesis b, involving the relationships between the C, N, and P pools and vegetation, was tested in two ways. First, differences in concentration of C, N and P between shrub and intershrub positions and among vegetation types for both depths (0-5 and 5-15 cm) were tested using analysis of variance and Student Newman-Keuls range tests. Second, multiple regressions were performed using plant cover to predict C, N, and P pools (expressed in  $\text{g/m}^2$ ), weighted by shrub cover. For hypothesis c, (relationships between soil texture and vegetation), I used the same statistical techniques and design as those described above for soil pools. Texture variables used as single dependent variables were percent clay, percent silt, and percent silt + clay. The relationship between net N mineralization data and vegetation (part of hypothesis e) was tested using ANOVA (SYSTAT

1984) testing for differences among vegetation types.

Principal components analysis and multiple regression techniques were used to examine the relationship between net N mineralization and all other variables (hypotheses d and e). The principal components analysis (SPSS/PC 1986) included all of those variables that were considered to have long-term temporal variability, such as soil texture, soil pools, and vegetation data. Principal components analysis removes the multiple-collinearity among variables, and re-expresses the variables as new orthogonal variables. These new variables (the principal components) and the climate variables (soil temperature and moisture) that have short-term variability were regressed against net N mineralization rates (SPSS/PC 1986). Regressions for each of the six months with 30-plot data (n=30), for the annual rates (n=30), and for all months together (n=180) were tested at the 5% significance level.

## Results

### Total carbon, nitrogen, and phosphorus

Carbon concentrations in both the 0-5 and 5-15 cm depths (Table 1) were significantly different among vegetation types and between shrub-intershrub positions. Carbon concentrations were highest in the ARTRV community, and lowest in the ARNO community. For the two drier communities (ARNO and ARTRW), under-shrub positions had higher C concentrations than between-shrub positions. There were no significant interactions between

vegetation type and shrub-intershrub position. When the carbon data were expressed as mass/area ( $\text{g/m}^2$ ) and weighted by shrub-intershrub position, there were significant differences among vegetation types for the 0-5 cm depth, but not for the 5-15 cm depth.

Total nitrogen (N) concentrations (Table 1) showed results similar to carbon, with significant differences among vegetation types and between shrub positions. N concentrations were highest in the ARTRV and lowest in ARNO soils, and were higher under shrubs than between in the two drier communities. There was no significant interaction between vegetation class and shrub position for N concentrations. When the N data were expressed as mass/area ( $\text{g/m}^2$ ), there were no significant differences among vegetation types for the 0-5 cm depth, but there were for the 5-15 cm depth.

Total phosphorus (P) concentrations ( $\text{mg/g}$ ) in the 0-5 cm depth were significantly different among vegetation types, but not between shrub positions, showing highest concentrations in the ARTRV plots and lowest in the ARNO plots. Total phosphorus concentrations in the 5-15 cm depth showed no significant differences among vegetation types or shrub positions. Phosphorus pools ( $\text{g/m}^2$ ) were not significantly different among vegetation types at any depth.

The C/N ratios (Table 1) were not significantly different among vegetation types, but were significantly higher under shrubs than between shrubs. The C/P ratios also were not

significantly different among vegetation types, although the ARTRV plots consistently had the highest C/P ratios. Under-shrub positions had significantly higher C/P ratios than did between-shrub positions.

Soil N, P, and C pools ( $\text{g/m}^2$ ) were regressed against vegetation cover data for each plot. Vegetation variables used were fractional cover for each of the 3 sagebrush shrubs, total grasses, total cushion plants, and bare ground. Carbon and nitrogen showed significant but weak correlations with the vegetation data and were most strongly correlated with total shrub cover (Fig. 2). Total phosphorus showed no significant correlations with vegetation data.

#### Soil texture

All soils were loamy sands and sands. Percent clay (Fig. 3a and b) for the 0-5 and 5-15 cm depths was not significantly different among vegetation types or between shrub positions. Percent silt, however, was significantly different among vegetation types at both depths, with the ARTRV plots having the highest and ARNO plots the lowest silt contents. Total fines (silt + clay) showed the same statistical pattern as silt.

Multiple regressions of plant cover on texture resulted in significance only for the silt and silt + clay variables. These two fractions were most strongly related to the cover of A. tridentata ssp. vaseyana and ssp. wyomingensis.

### Field moisture and temperature

Weekly measurements of soil moisture and temperature showed seasonal trends (Figs. 4a and b) that were strongest in the ARTRV plots. Soil moisture was significantly different among vegetation types for all dates between May 10 and July 9 (days of year 130 and 190). ARTRV plots had consistently higher soil moisture. There were no significant differences between shrub-intershrub positions.

Soil temperature (Fig. 4b) showed a 20°C amplitude for all vegetation types between early May and early October (days of year 130 to 280). Soils from ARTRV plots had significantly lower soil temperatures intermittently throughout this period, and the ARNO plots had significantly higher soil temperatures. Beginning in early July, there was a significant effect of shrub-intershrub position, with under-shrub positions in all vegetation types having soil temperatures 1 to 2 degrees lower than between-shrub positions.

### In situ incubations

During the late spring and early summer months (June 1985, May and June 1986), soil moisture in the buried bags was high, decreasing during the summer months and reaching a minimum in August or September. Soil moisture in the bags for July 1985 was higher than usual for this month because the sampling occurred immediately after a large rainstorm. Significant differences among vegetation types occurred only during the months of highest



soil moistures, June 1985 and May and June 1986. Shrub-intershrub position showed no significant differences in soil moisture.

Initial ammonium content in the buried bags (Fig. 5b) showed a seasonal trend, peaking in the soils of the ARNO vegetation type in winter '85-86, of the ARTRW type in April of 1986 and in the ARTRV soils in June of 1986. Significant differences among vegetation types in initial ammonium content occurred in winter of 1985-6 and in October of 1986. Ammonium concentrations (mg/kg) were generally higher under shrubs than between shrubs for all vegetation types, but the trend was significant only in winter, April, May, and June of 1986.

Initial nitrate contents also showed strong seasonal trends, with the highest values in spring and early summer (Fig. 5c). Nitrate was highest in the ARNO plots in April 1986, in the ARTRW plots in May 1986, and in the ARTRV plots in June 1986. Nitrate showed the greatest seasonal amplitude in the ARTRV plots. Significant differences among the vegetation types occurred in June and August 1985 and in May 1986. Shrub-intershrub position had no significant effect on nitrate.

Net nitrification rates were nearly always greater than 90% of the total net N mineralization rates. A strong seasonal pattern in net N mineralization was evident only in soils of the ARTRV vegetation type, where the rates were highest in late spring and early summer (Fig. 5d). Significant differences among vegetation types were found during the months of June and July

1985, and May and June 1986. There were no significant differences between shrub-intershrub positions. However, when there were peaks in net N mineralization, there were consistently higher rates under shrubs than between shrubs.

Total annual N mineralization for the 3 vegetation types was estimated by summing net N mineralization for all months for one year (June 1985 - May 1986) (Fig. 6). These data show much higher N mineralization in the ARTRV vegetation than in the ARTRW or ARNO vegetation.

#### Principal components analysis

The principal components analysis of the vegetation, texture, and C, N, and P data (variables listed in Table 2) indicated that these variables were interrelated. The first four principal components accounted for 77.3 % of the total variance in the data. Communalities of the variables, representing the fraction of variability shared with the other variables through the principal components, were all over 53%. The first principal component (PC1) accounted for 38.7% of the variance, and was primarily a function of the vegetation variables and total nitrogen content of soils (Table 2). PC2 was primarily a function of the cover of A. nova and A. tridentata ssp. wyomingensis and the texture variable, silt + clay. PC3 was primarily a function of total phosphorus, and PC4 of the silt + clay variable.

For each of the six periods of June, July, August, and

winter 1985 and April and May 1986, net mineralization rates were regressed on the four principal components scores and soil moisture for the incubation. The form of the regression equations was:

$$\begin{aligned} \text{net N mineralization / 30 days} = \\ \text{constant} + a_1(\text{PC1}) + a_2(\text{PC2}) + a_3(\text{PC3}) + \\ a_4(\text{PC4}) + a_5(\text{soil moisture}) \end{aligned}$$

The regressions predicting net N mineralization were significant for all periods except winter and April (Table 3). PC1 was the most important independent variable in the regression for net N mineralization in June, August, and winter, and moisture contributed most to the regression in June and May, the periods when soil moisture was high and most variable across the landscape.

Annual net N mineralization rates were regressed on the four principal components and the average moisture of the buried bags over the year. The regression was highly significant ( $p = .0001$ ) ("annual rate", Table 3). Average moisture did not contribute significantly to the regression; PC1 was the only significant independent variable.

In a final analysis, the monthly buried bag data were combined into a single regression, using all plots for all months ( $n=180$ , 30 plots x 6 time periods). I assumed that temporal

replicates from the plots were independent for this analysis. Monthly means of daily maximum air temperatures ( $T_{\max}$ ) could be included in the regressions (Table 3):

$$\begin{aligned} \text{net N mineralization / 30 days ("all year")} = \\ \text{constant} + a_1(\text{PC1}) + a_2(\text{PC2}) + a_3(\text{PC3}) + \\ a_4(\text{PC4}) + a_5(\text{soil moisture}) + a_6(T_{\max}) \end{aligned}$$

The regression was highly significant ( $p < .0001$ ), with the variables temperature, moisture, and PC1 contributing significantly to the regression ("all year", Table 3).

## Discussion

### Variation in soil microclimate (hypothesis a)

Soil microclimate had significant landscape and seasonal variability, as predicted. Spatial patterns in soil moisture were apparent during spring and early summer, the period during and following snowmelt, but did not occur at the shrub-intershrub scale. Soil temperature varied both across the landscape and between shrub positions intermittently throughout the summer, suggesting that vegetation insulated the soil during warm summer days.

Soil microclimate can exert a significant control over turnover processes (Matson and Vitousek 1981, MacDuff and White 1985, Schimel and Parton 1986). In this system, increases in

field rates of net N mineralization generally correspond with periods of high soil moisture.

Variation in total soil nutrient pools with vegetation  
(hypothesis b)

I predicted that patterns in plant productivity and erosion would result in increasing C, N, and P pools with increasing vegetation cover and with downslope and leeward position. Carbon, N, and P increased with vegetation cover (or cover class), showing highest values in ARTRV communities typical of leeward, high snow-deposition areas. Concentration data exhibited more significant differences than mass data ( $\text{g/m}^2$ ) because of variability in bulk density. Increases in organic matter and C, N, and P with downslope position have been documented by many authors (Aandahl 1948, Malo et al. 1974, Voroney et al. 1981, Schimel et al. 1985a, b, c). Many of these authors attribute the pattern to processes that transport organic matter downslope (Reiners 1983). Two mechanisms of physical transport are likely at Stratton, aeolian transport and long-term run-off. No data on long-term run-off are available, but aeolian redistribution of soil organic matter during winter does occur (spring snow content of  $3900 \text{ g/m}^2$  in toeslopes vs.  $200 \text{ g/m}^2$  on summits, Reiners, unpubl. data). However, the intense gradient in soil moisture, plant biomass, cover, and apparent productivity across the landscape suggests that in situ accumulation of organic matter is the more important process causing landscape

patterns for C and N (Schimel et al. 1985). Phosphorus, with no biological input process, varies only as a consequence of physical transport.

Total C and N showed shrub-intershrub variability, with higher accumulations of organic matter under shrubs in the two shorter shrub types. Shrub-intershrub variation in total soil pools and in available N have been documented in many arid and semi-arid shrublands (Charley and West 1975, Tiedemann and Klemmedson 1973, Lajtha and Schlesinger 1986, Doescher et al. 1984, and Klopatek 1987). In this study, the effect of shrubs on nutrient accumulation did not result in significant differences in N mineralization rates, although during high mineralization periods there was consistently higher N mineralization under than between shrubs and other studies at the same site have indicated higher mineralization rates under shrubs than between (Burke et al. 1987). Specific N mineralization rates, or the amount of N mineralized per unit total N, are higher between shrubs than under, suggesting that immobilization is a more important process under shrubs. This corresponds with results from a separate study showing higher microbial biomass under than between shrubs (Burke et al. 1988).

#### Variation in soil texture (hypothesis c)

I hypothesized that over the long term, fine soil material removed from sites exposed to wind and water erosion accumulates in deposition sites. Soil texture data indicate that slope

processes have caused a slight accumulation of fine material in leeward and downslope positions, a well-documented process in many systems (Jenny 1980). Although the clay fraction did not increase with vegetation cover, silt and total fine (silt + clay) fractions were slightly, though significantly higher in the ARTRV vegetation type characteristic of toeslopes than in the ARNO vegetation type characteristic of ridgetops. Clay contents of the soils may be so low that movement is not discernible.

The lack of pattern in soil texture with shrub-intershrub position was surprising. Field observations suggest that in dry windswept areas, both net deflation between shrubs, and net accumulation of organic matter and fines under shrubs are occurring. Possibly the 0-5 cm cores were too deep to detect what is only a surface phenomenon and of less importance than surface appearances would suggest.

In many systems, soil texture influences soil processes through the protection of organic matter by both adsorption and aggregation, thereby slowing turnover and effectively increasing soil organic matter (Jenkinson 1977, Sorenson 1981, Paul 1984, Schimel et al. 1985c, Parton et al. 1987). In addition, fine soil increases the water-holding capacity of soils, such that soil texture interacts with microclimate to control soil turnover processes (Van Veen et al. 1985, Schimel and Parton 1986). These mechanisms could be important in the sagebrush system, but because there is so little variability in clay content at Stratton, the control of organic matter turnover by clay is not

apparent.

#### Integration of static ecosystem properties through principal components analysis

The principal components analysis indicates that ecosystem properties that are the long-term result of landscape variability are highly intercorrelated. Only four principal components were required to describe most of the variability in vegetation, soil nutrient pools, and soil texture. The principal components, describing properties that vary in space and change slowly, may represent indices of substrate availability for N mineralization. Specifically, PC1, accounting for much of the variation in the data set, and especially in vegetation and N, should be closely related to N mineralization rates.

#### Controls of in situ mineralization rates (hypotheses d-e)

To what extent do substrate availability and microclimate control in situ net N mineralization, and how do these factors vary in time? Probabilities and r values from monthly regressions of principal components and soil moisture on monthly net N mineralization rates (Table 3) are useful in separating these effects, even where the regression accounts for a small portion of the variance. Regressions indicate that both substrate availability and soil moisture control net N mineralization rates at some time of the year. For June and July of 1985, both PC1 (representing an axis of substrate availability) and soil moisture were necessary to accurately



predict net N mineralization. For August and winter, soil moisture did not vary across the landscape, and so PC1 correlated well with observed rates. April 1986 was a very cold month, and none of the principal components or soil moisture data correlated with net N mineralization; soil temperature may have been the main control of net N mineralization during that time. During May, soil moisture and the two principal components PC3 (expressing much P variation) and PC4 (expressing soil texture) were significantly related to net N mineralization. During this month of maximum water availability, components of substrate quality other than N were apparently limiting to net N mineralization rates. Regressions for all months of the principal components, soil moisture, and mean daily maximum air temperature on net N mineralization rates indicate that monthly rates were simultaneously controlled by substrate availability, soil moisture, and temperature. The relationships in Figures 7a and b show that at high moistures and temperatures, net N mineralization responded much more to increases in PC1 than at low temperatures and moistures. Similarly, at high values of PC1, net N mineralization had a greater response to increases in temperature and moisture than at low values of PC1. Thus, where substrate was limiting, in ARNO and ARTRW communities, temperature and moisture had only a moderate effect on net N mineralization. When soil moisture or temperature were limiting, in midsummer and winter, substrate availability had only a

moderate effect on net N mineralization. Significant landscape variation in N mineralization only occurred during the short intervals when soil moisture and temperature were not limiting.

Regressions of the principal components and soil moisture on the annual nitrification rates indicate that rates were not related to average annual soil moisture. This is probably because the principal components better represent long-term influence of soil microclimate as it varies continuously across the landscape than do averages of annual soil moistures. Annual mineralization rates in this sagebrush landscape can be adequately predicted from vegetation and soil pool information.

In summary, nutrient dynamics in semiarid sagebrush steppe are controlled by a complex of factors that vary spatially and temporally. The dynamic control over N mineralization by soil microclimate is clear; ninety percent of annual N mineralization occurs in spring and early summer when soil moisture is adequate and soil temperatures are high. During this period, organic matter plays a critical role in controlling N mineralization, as shown by the importance of the first principal component in regressions of June and July 1985 mineralization. Thus the effect of organic matter, a relatively stable property, on N mineralization is regulated by the more dynamic soil microclimate.

Natural variability present in the sagebrush landscape allows controls over N mineralization to be separated. Principal components analysis provides a powerful tool for integrating

information about ecosystem properties that have similar spatial and temporal scaling. The resulting independent axes are useful for examining relationships among hypothesized controls and ecosystem processes. A caveat for this approach is that only correlative relationships can be tested, with inference to cause and effect. These techniques may be extended to similar systems that are dominated by strong seasonal and spatial patterning.

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## Figure Legends

Figure 1. Conceptual model of the control of sagebrush ecosystem properties related to N turnover. Hypotheses concerning the nature of relationships a-e are described in this paper. Dotted lines denote relatively minor feedbacks.

Figures 2a - b. Total C, N, and P versus total shrub cover in three sagebrush vegetation types. Best regressions of these pools versus continuous plant species cover data are:  $C \text{ (g/m}^2\text{)} = 3264 - 13.72 (\% \text{ bare ground})$ , ( $R = .49$ ,  $p = .05$ );  $N \text{ (g/m}^2\text{)} = 198.2 + 1.7(\% \text{ A. tridentata ssp. vaseyana}) + 1.8(\% \text{ A. nova})$ , ( $R = .63$ ,  $p = .001$ );  $P \text{ (g/m}^2\text{)} = 76.0 - 2.1(\% \text{ cushion plants})$ , ( $R =$

Figures 3a - b. Soil texture in a) surface (0-5 cm) and b) subsurface (5-15 cm) soils for 3 sagebrush vegetation types stratified by shrub-intershrub position. VB = A. tridentata ssp. vaseyana vegetation, between shrubs, VU = under shrubs; WB = A. tridentata ssp. wyomingensis vegetation, between shrubs, WU = under shrubs; and NB = A. nova vegetation, between shrubs, NU = under shrubs. Error bars represent one standard error of the mean.

Figures 4a - b. Soil moisture and temperature in surface soils (10 cm and 0-15 cm, respectively) in 3 sagebrush vegetation types (between-shrub positions) for the 1986 growing season. Error bars represent the largest standard error of the mean in the data set. Asterisks show times at which differences among vegetation types were significant ( $p < .05$ ).

Figures 5a - d. Percent moisture, initial ammonium and nitrate, and net N mineralization rates of soils of in situ incubations from June 1985 to October 1986 in 3 sagebrush vegetation types. Error bars represent the largest standard error of the mean in the data set, and asterisks show times at which differences among vegetation types were significant ( $p < .05$ ).

Figure 6. Annual net N mineralization estimates in in situ incubations of soils from 3 sagebrush vegetation types. Average areal estimates are calculated from specific rates measured under and between shrubs and corrected for areas occupied by shrubs. The two components of net N mineralization, net ammonium production and net nitrification, are shown separately. VASEY = A. tridentata ssp. vaseyana, WYO = A. tridentata ssp. wyomingensis, NOVA = A. nova.

Figures 7a - b. Net N mineralization of sagebrush soils as a function of soil moisture and a principal component (PC1) integrating the vegetation and soil nutrient pools, and (b) as a function of temperature and PC1. As PC1 increases, A. tridentata ssp. vaseyana cover, grass cover, and total N increase, and cushion plant cover decreases. Data from 5 months and 1 winter period of in situ incubations were used to construct this surface, with a total of 180 points. See text for description of principal components analysis.

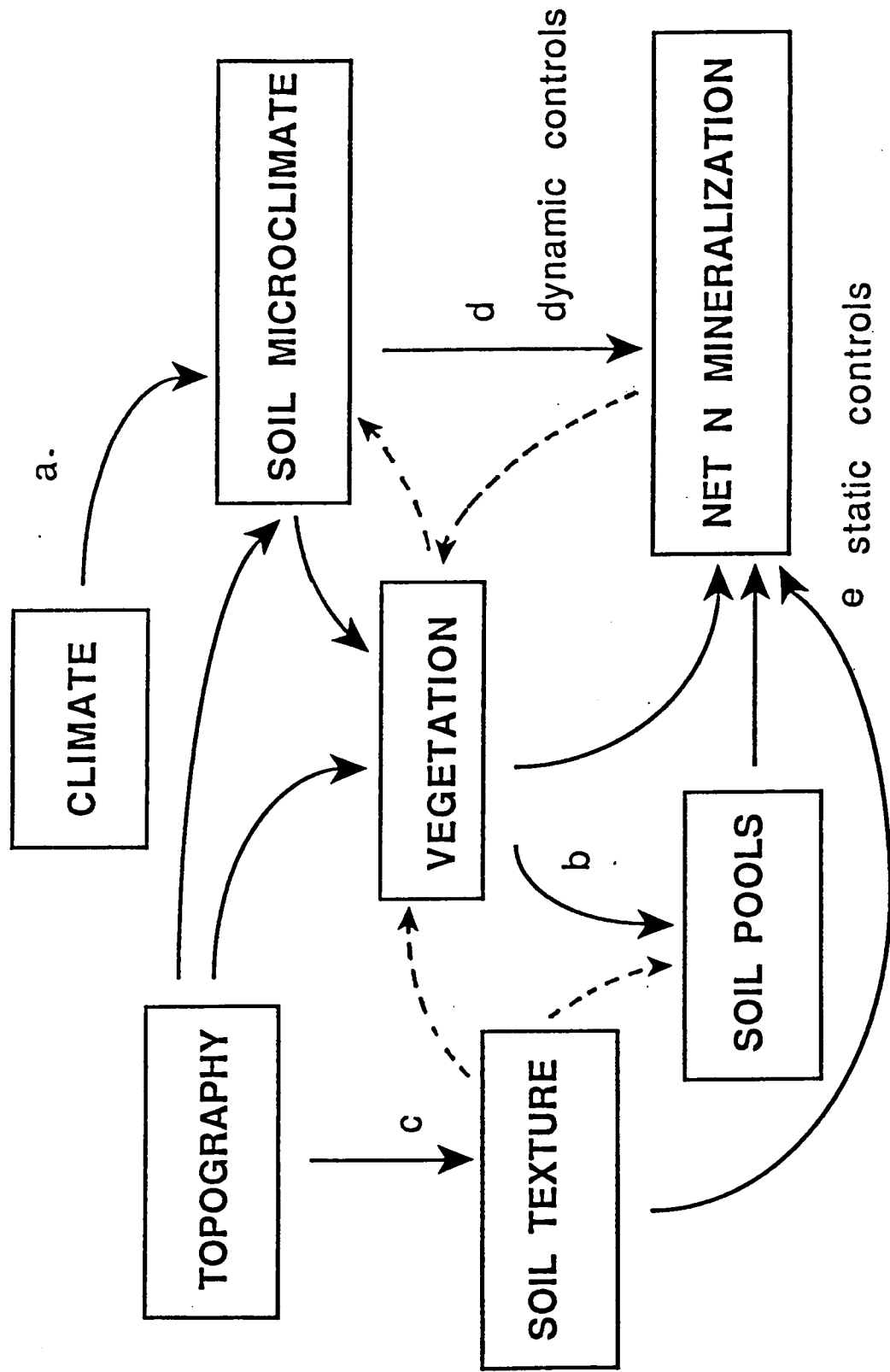


Figure 1.

Figure 2.

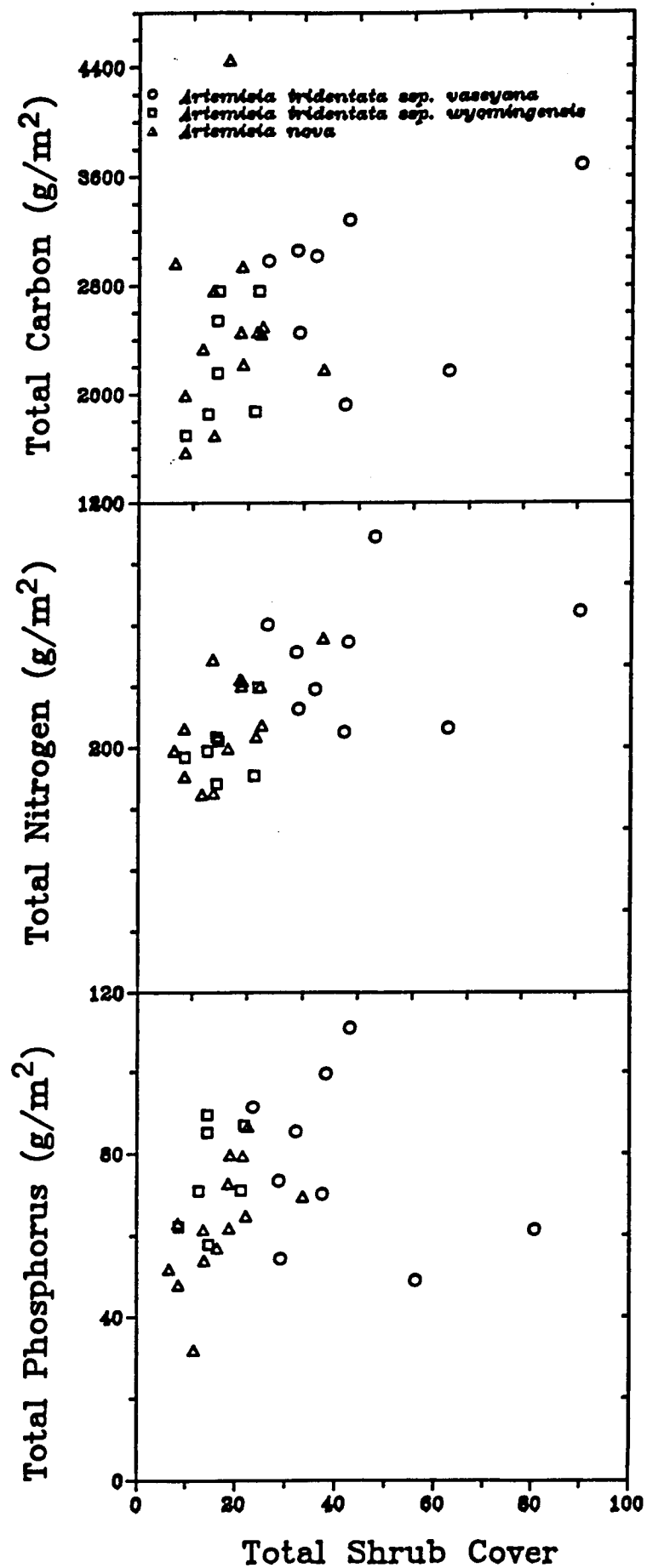




Figure 3.

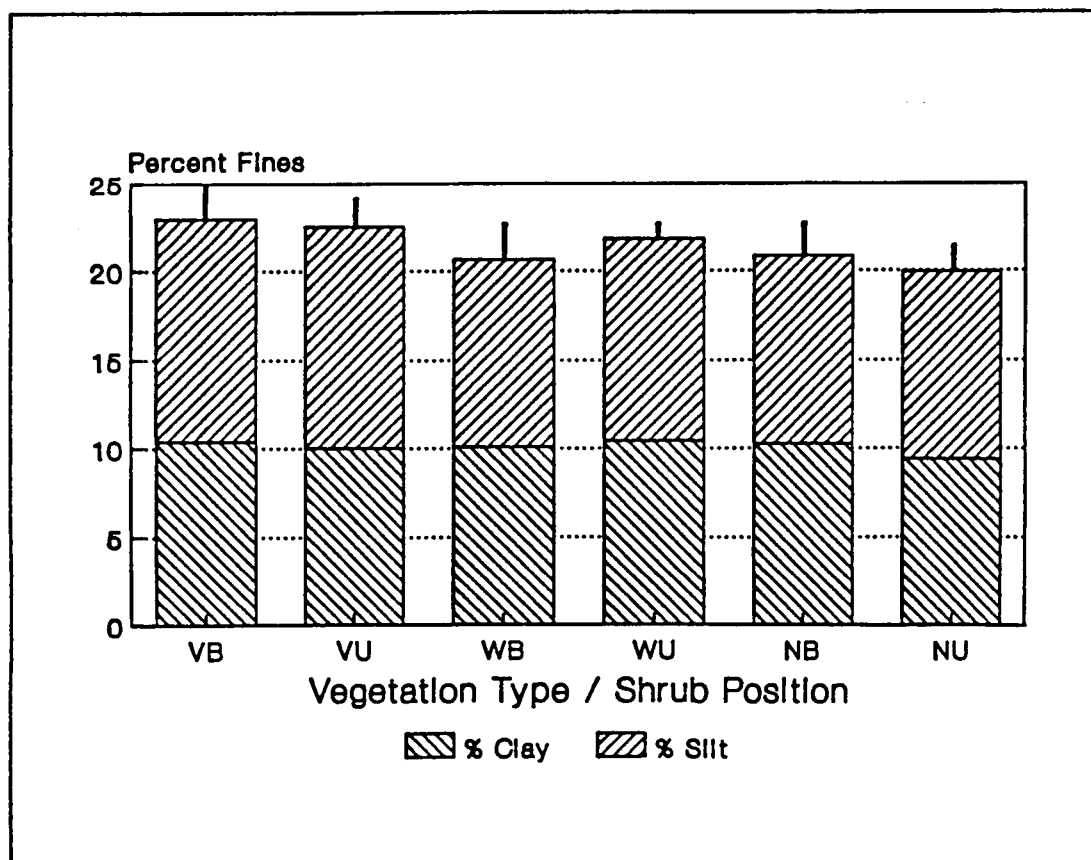
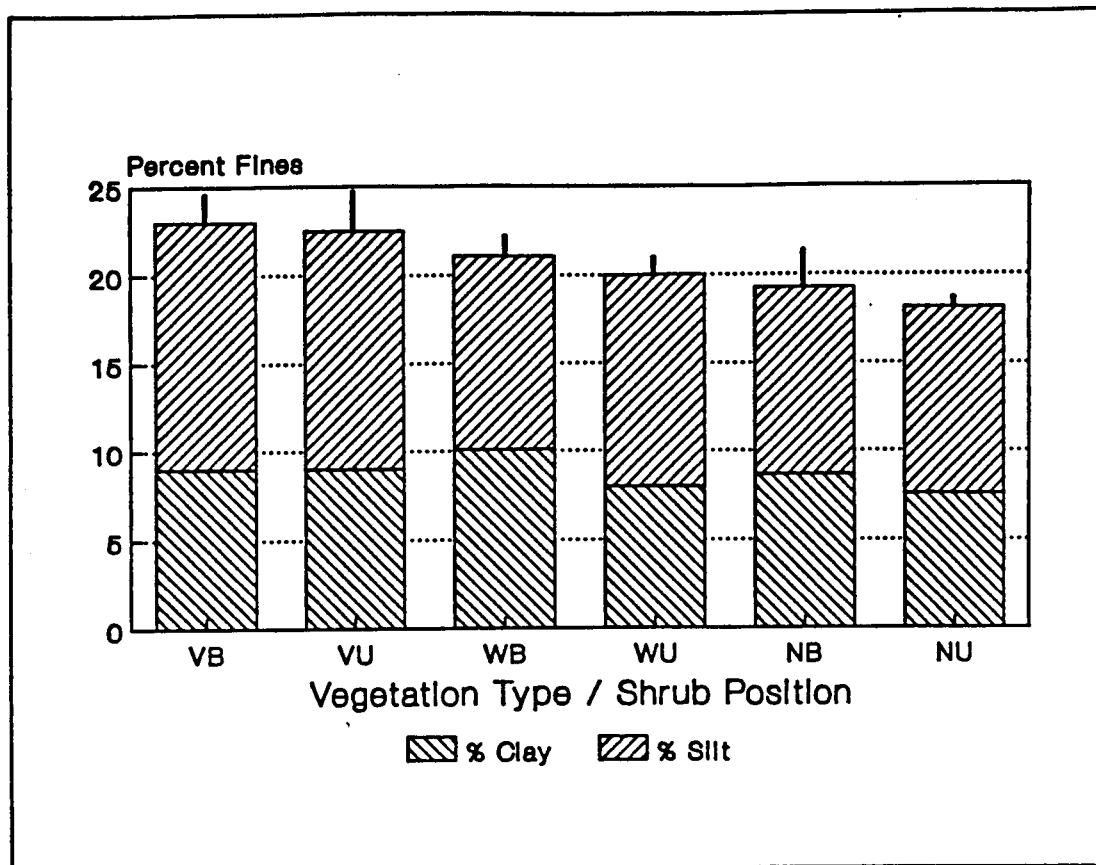


Figure 4.

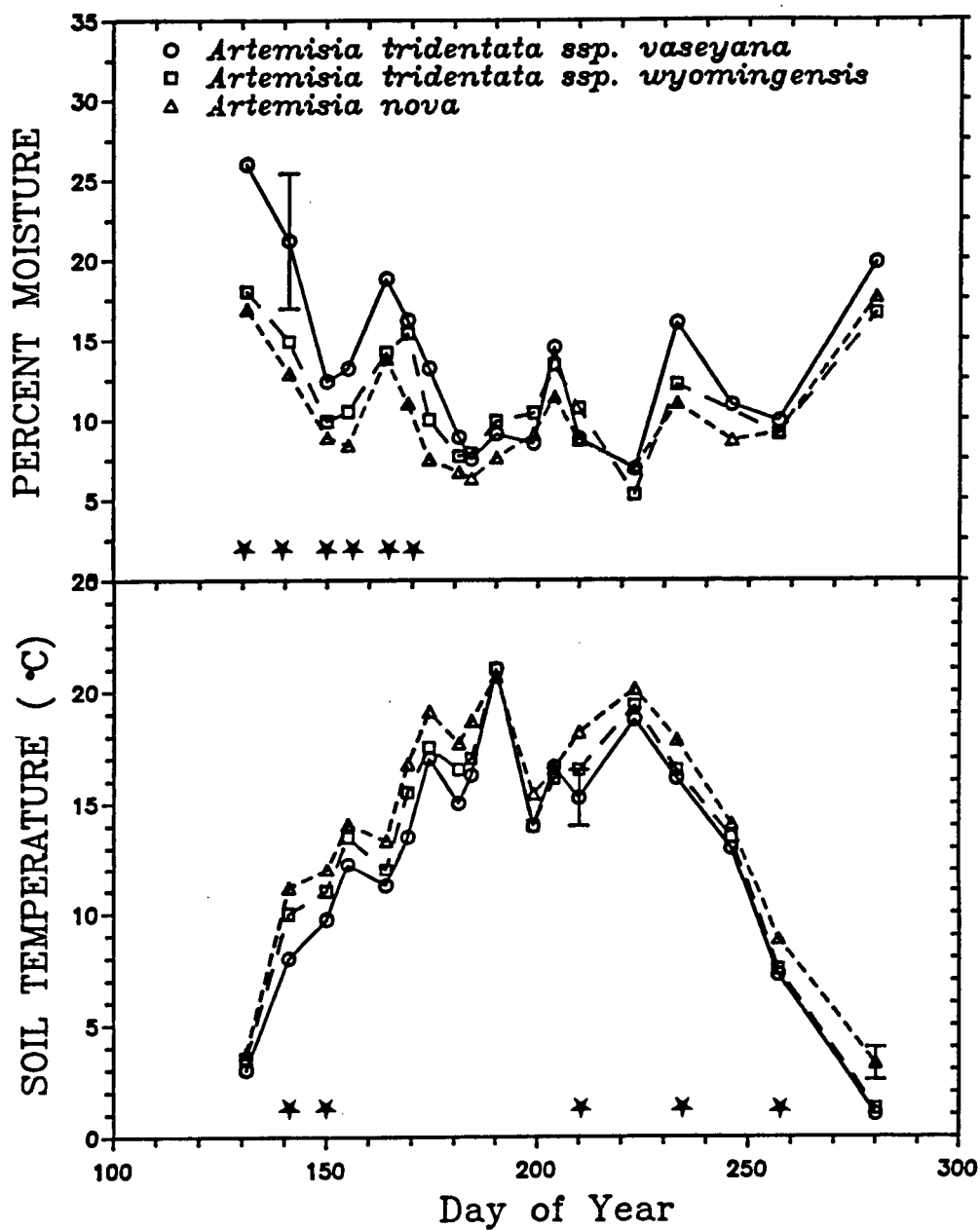


Figure 5.

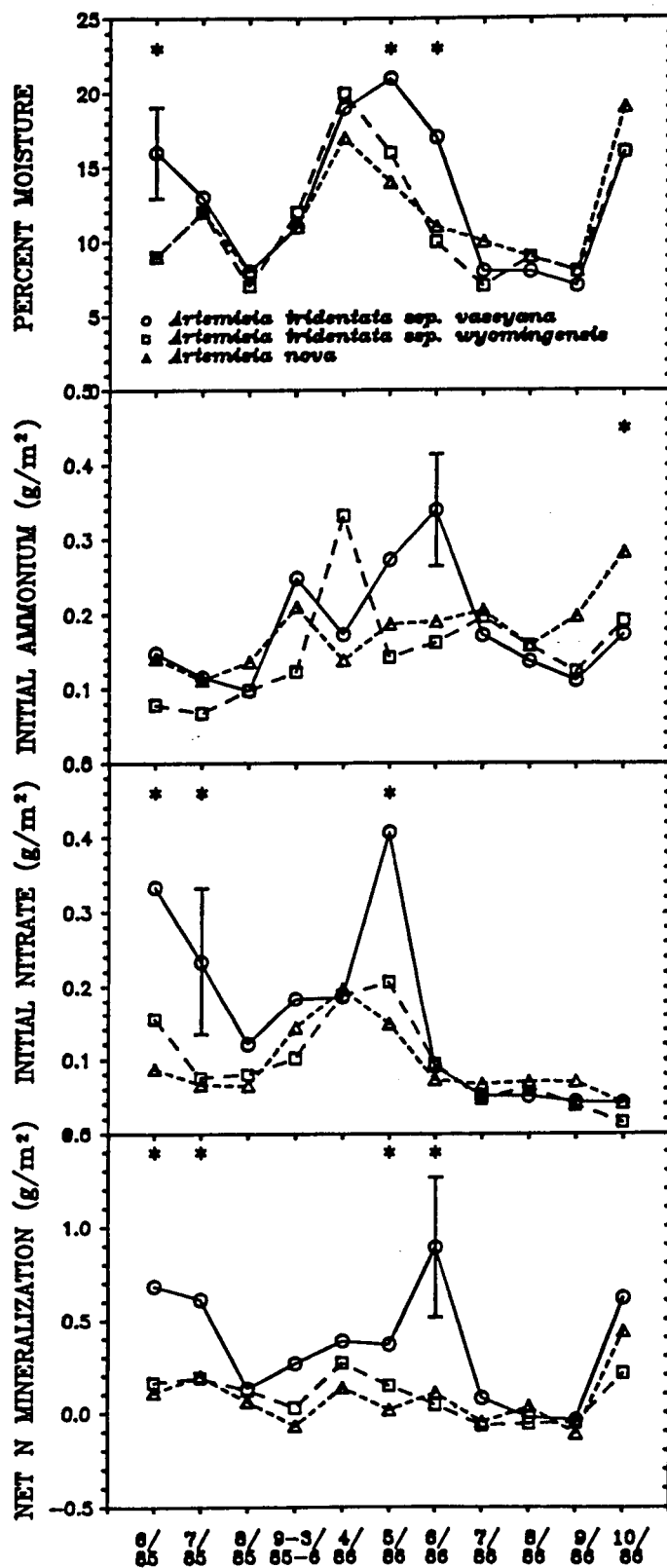
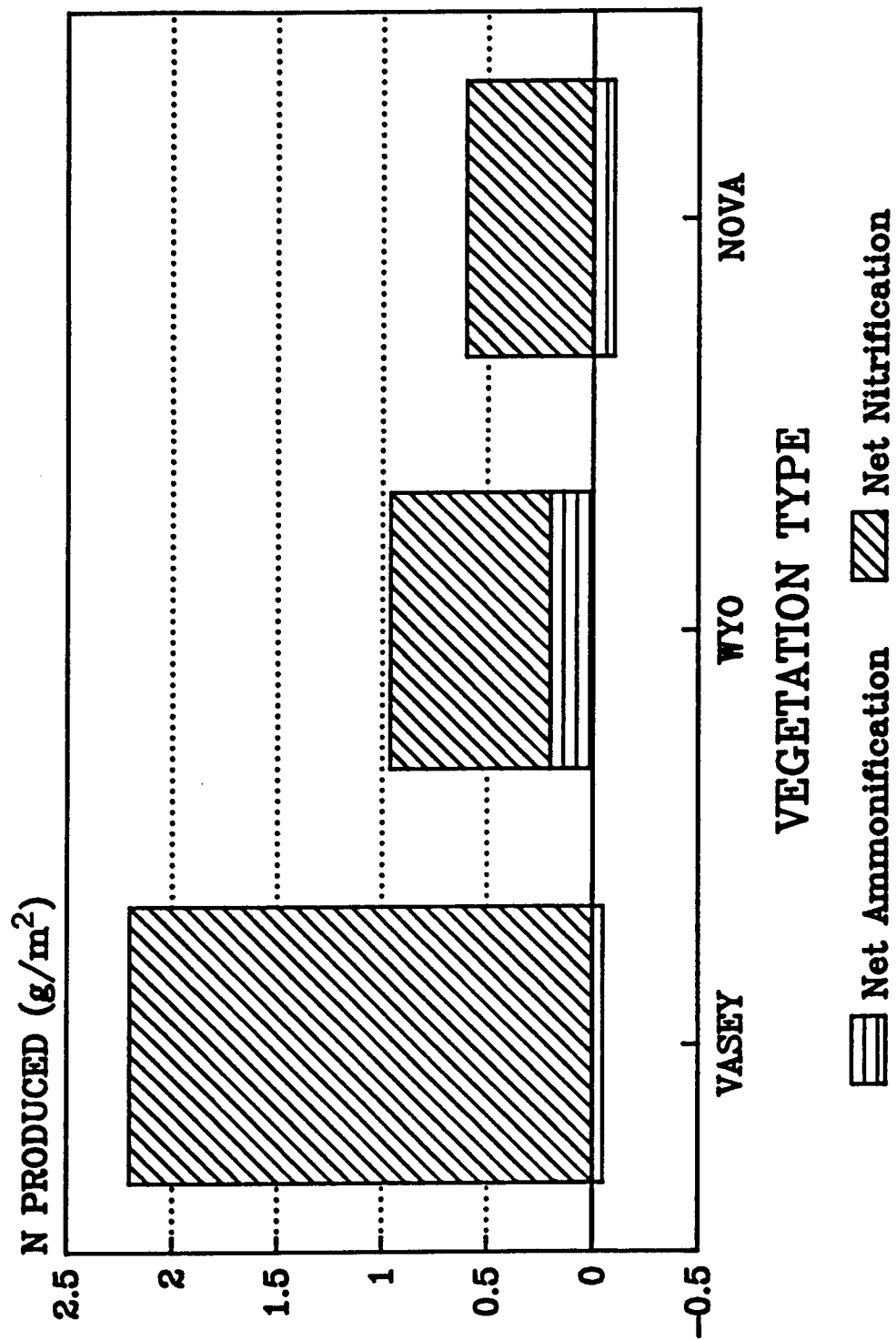


Figure 6.



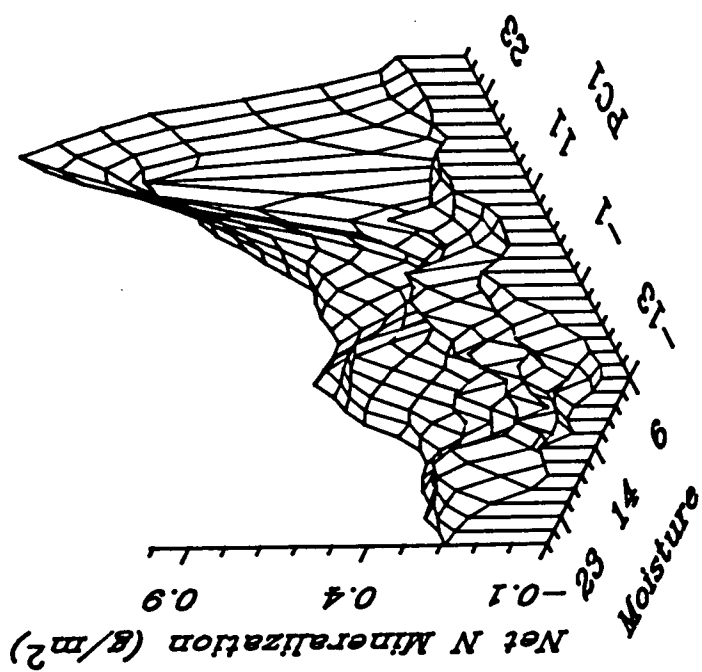
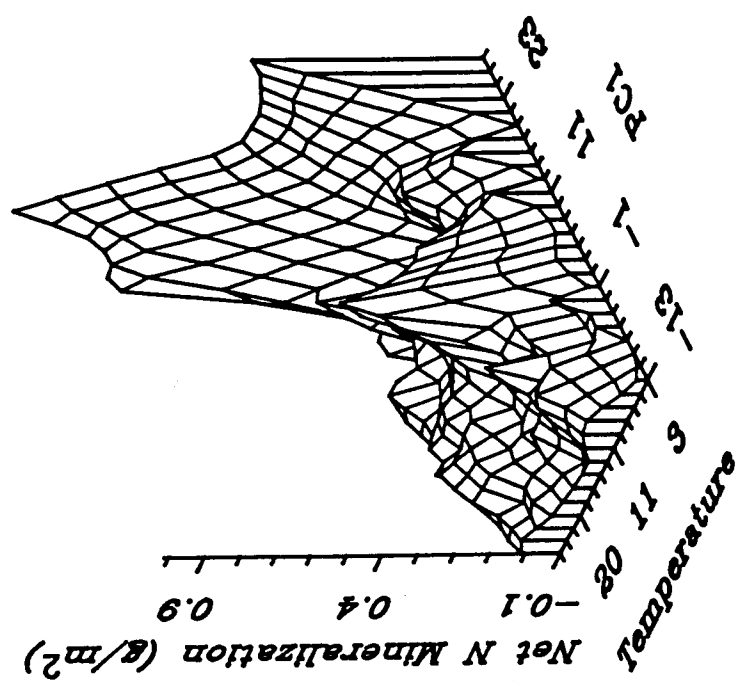


Figure 7.

Table 1. Soil C, N, and P data from the three sagebrush vegetation types and two different depths. Significance values are probabilities from an ANOVA testing for effects of vegetation type and shrub-intershrub position on soil nutrient concentrations for each depth. Values in parentheses are standard errors of the means.

Vegetation type	Shrub-intershrub position	Depth (cm)	C		N		P		C/N (w/w)	C/P (w/w)
			(%)	(g/m <sup>2</sup> )	(mg/g)	(g/m <sup>2</sup> )	(mg/g)	(g/m <sup>2</sup> )		
<u>A. tridentata</u> <u>ssp. vaseyana</u>	Between shrubs	0-5	2.8 (0.4)	1228 (181)	2.6 (0.4)	85 (22)	0.59 (0.15)	25 (7)	10.8	47.5
		5-15	1.6 (0.3)	1846 (630)	1.9 (0.3)	206 (48)	0.53 (0.08)	60 (18)	8.4	30.2
	Under shrubs	0-5	2.6 (0.1)	1331 (290)	2.1 (0.6)	85 (22)	0.59 (0.15)	25 (7)	12.4	44.1
		5-15	2.0 (0.4)	1423 (250)	2.1 (0.2)	188 (34)	0.52 (0.12)	52 (17)	9.5	38.5
<u>A. tridentata</u> <u>ssp. wyomingensis</u>	Between shrubs	0-5	1.5 (0.1)	791 (73)	1.3 (0.1)	68 (4)	0.48 (0.02)	25 (1)	11.7	31.3
		5-15	1.4 (0.3)	1532 (271)	1.4 (0.3)	132 (8)	0.41 (0.04)	45 (10)	10.0	34.1
	Under shrubs	0-5	2.2 (0.1)	1098 (81)	1.7 (0.1)	87 (4)	0.53 (0.02)	27 (1)	12.9	41.5
		5-15	1.6 (0.2)	1325 (223)	1.6 (0.4)	117 (17)	0.47 (0.04)	40 (8)	10.0	34.0
<u>A. nova</u>	Between shrubs	0-5	1.5 (0.1)	816 (55)	1.5 (0.0)	80 (3)	0.40 (0.02)	22 (1)	10.0	37.5
		5-15	1.6 (0.1)	1595 (197)	1.5 (0.1)	136 (10)	0.44 (0.03)	40 (4)	10.6	36.4
	Under shrubs	0-5	1.9 (0.1)	1161 (91)	1.6 (0.1)	93 (6)	0.40 (0.02)	24 (1)	11.9	47.5
		5-15	1.8 (0.1)	1706 (119)	1.6 (0.1)	162 (9)	0.43 (0.04)	42 (6)	11.2	41.9
Significance (p) of vegetation type		0-5	0.000	0.074	0.000	0.127	0.000	0.110	0.324	0.307
		5-15	0.056	0.499	0.000	0.007	0.368	0.170	0.097	0.473
Significance (p) of shrub position		0-5	0.008	0.499	0.289	0.539	0.830	0.506	0.049	0.037
		5-15	0.037	0.787	0.065	0.942	0.497	0.797	0.423	0.491
Significance (p) of shrub x vegetation		0-5	0.372	0.756	0.146	0.053	0.703	0.393	0.409	0.604
		5-15	0.956	0.763	0.967	0.522	0.481	0.383	0.721	0.309

Table 2. Results of a principal components analysis on all vegetation (species % cover) data, soil nutrient data (0-15 cm, C, N, and P pools), and soil texture data. Loadings listed are simple correlations of the original variables with the new principal components, PC1-PC4. Communalities are the percent of the variability shared with other variables through the principal components. The principal components account for 77.3% of the variability in the entire data set. The correlation matrix had a determinant of 0.00018.

Variable	Loadings				Communality
	PC1	PC2	PC3	PC4	
% cover bare ground	-0.96	0.01	0.14	0.13	0.96
% cover <u>A. tridentata</u> esp. <u>vaseyana</u>	0.92	0.01	-0.31	0.05	0.95
% cover <u>A. tridentata</u> esp. <u>wyomingensis</u>	-0.23	-0.67	0.42	-0.22	0.73
% cover <u>A. nova</u>	-0.46	0.78	0.12	-0.03	0.84
% cover grass	0.66	-0.30	-0.05	0.10	0.54
% cover cushion plants	-0.67	-0.06	-0.36	0.46	0.80
% silt + clay	0.22	-0.54	-0.05	0.72	0.86
Total carbon	0.31	0.28	0.28	0.48	0.53
Total nitrogen	0.63	0.45	0.37	0.22	0.79
Total phosphorus	0.24	-0.04	0.88	0.08	0.74

Table 3. Results of regression analyses predicting net N mineralization from the four principal components, soil moisture, and soil temperature. See text for the forms of the regressions.

Nitrate production period	N	R	P	Significance of effect						Tmax <sup>3</sup>
				PC1	PC2	PC3	PC4	Moist <sup>1</sup>	Moist <sup>2</sup>	
June 1985	30	0.78	0.0005	0.0001	0.56	0.28	0.58	0.11		
July 1985	30	0.62	0.04	0.04	0.32	0.01	0.87	0.27		
August 1985	30	0.68	0.01	0.004	0.91	0.97	0.11	0.0040		
Winter 1985-86	30	0.53	0.16	0.01	0.81	0.55	0.92	0.93		
April 1986	30	0.42	0.52	0.97	0.41	0.13	0.50	0.51		
May 1986	30	0.69	0.007	0.46	0.57	0.08	0.03	0.05		
Annual rate 1985-86	30	0.81	0.0002	0.0000	0.61	0.24	0.88		0.83	
All year <sup>4</sup>	180	0.80	0.0001	0.0000	0.50	0.03	0.55	0.0009		0.000

<sup>1</sup>Soil moisture of buried bags during incubation.

<sup>2</sup>Average soil moisture of buried bags during entire year.

<sup>3</sup>Monthly average of daily maximum air temperature.

<sup>4</sup>All monthly rates run in one analysis.